# AN ANALYSIS OF THE EFFECT OF COMPETITION ON DAPHNID SPECIES DIVERSITY, OR WHY ARE THERE SO FEW SPECIES OF DAPHNIA IN THE SUBTROPICS AND TROPICS?

by

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JEFFERY ALLEN FORAN

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This study shows that *Daphnia laevis* Birge outcompetes *Daphnia magna* Straus under food (*Chlamydomonas reinhardi*) limited conditions at three constant temperatures. Further, the competitive superiority of *D. laevis* is predictable from its life history characteristics at 21° and 27°C. *D. laevis* has a higher $r_m$ than *D. magna* at both temperatures, which is a result of the ability of individuals to begin reproduction at an earlier age than *D. magna* individuals. At 15°C, neither species has a fitness advantage (reproductive component), primarily because both species begin reproduction late in life. Yet, *D. laevis* is still able to outcompete *D. magna* at 15°C.

The reproductive and competitive abilities of *D. laevis* are used, along with temperature and algal data from subtropical and tropical aquatic systems, to show why these systems likely support a zooplankton community that exists near carrying capacity. These data and comparable data from temperate systems are then used to explain why subtropical and tropical aquatic systems typically have only a few, small body-sized zooplankton, and generally no daphnid species.

# CHAPTER 1
# INTRODUCTION

## Background

The distributions of tropical and subtropical members of the genus *Daphnia* are poorly described compared with distributions of most temperate cladocera. Brook's (1957) monograph provides detailed information on daphnid species distributions in temperate North America. Unfortunately, there are no such syntheses for tropical regions. Some data do exist, however, and the conclusions drawn from these are simply that daphnid species diversity is greatly reduced in tropical regions, and that body sizes of the few existing tropical species are considerably smaller than those of temperate daphnids.

Hebert (1978) has reviewed early work from Lake Toba in Sumatra, the Chambri Lakes in Papua, New Guinea, and some African lakes. Only one or two species of the genus *Daphnia* have been collected in any of these lakes. *D. lumholtzi* and *D. carinata* have been found in the well-studied lakes and reservoirs of Sri Lanka (Fernando 1980a), while *D. laevis* is the only daphnid found in Lake Naivasha, Kenya, a lake that has no vertebrate and few invertebrate zooplanktivores (Mavuti and Litterick 1981). Also in Africa, Lakes Mutanda, Bunyonyi and Mulehe have three, one, and zero species of *Daphnia*, respectively (Green 1976), while Lakes Kotto and Soden, and Barombi Mbo and Mboandong are entirely without cladocera (Green 1972). Evidence showing decreased tropical daphnid diversity and decreased body sizes is supported in many other works. D. barbata (1 mm length) in Lake George, Uganda (Burgis 1973), and D. lumholtzi (1.3 mm length) in Lake Albert (Green 1976) are examples. The ranges of these species are limited to the east African plateau region where distinct seasons occur. At the same latitude, in the seasonally nonvarying evergreen forest zone of west Africa, there are no species of Daphnia (Dumont 1980). Fernando (1980b) has reviewed much of the literature available that describes tropical southeastern Asian daphnid distributions and concludes that the genus there is also depauperate. Finally, the lowland tropical lakes of the Peten region of Guatamala have no Daphnia species and a generally reduced cladoceran assemblage (Deevey et al. 1980).

Although subtropical data are very scarce, there appear to be only two species of Daphnia in subtropical Florida, D. ambigua and D. laevis (Nordlie 1976; Crisman et al. 1979; Bays and Crisman 1983; Wyngard et al. 1982), while Lake Chilwa, Malawi, and Lake Sibaya, South Africa, have no daphnid species (Kalk et al. 1979; Allanson 1979). Temperate comparisons, however, are very abundant and include common examples where three to six species of Daphnia may occur in a single lake (Tappa 1965; Anderson 1974; Edmondson and Litt 1982). Temperate zone lakes and ponds also abound with large daphnid species including D. magna, D. pulex, and D. middendorffiana (Brooks 1957; Anderson 1974; Hebert 1978).

Hebert (1978) and others (Fernando 1980a, 1980b, 1980c; Lynch 1977) have suggested that high temperatures may limit the distribution of large bodied cladocera, particularly within the genus Daphnia. Yet, as I will show in this paper, temperatures up to 27°C, a temperature higher than occurs in some tropical lakes (Lewis 1979; Moss 1980; Green 1976), are not lethal to and, in fact, enhance fecundity of a large, temperate daphnid species.

Food quality and availability may play a major role in influencing cladoceran distributions. Fernando (1980a) has suggested that, in tropical lakes, there is frequently an abundance of blue-green algae, many species of which are generally inedible and may on occasion be toxic to certain zooplankton (Porter 1973; Porter and Orcutt 1980). However, Lewis (1978a) showed that Cyanophyta made up only 19% of the total algal biomass, while over 70% was composed of the Chlorophyta and Bacillariophyta in tropical Lake Lanao. Tropical lakes in general do not show any evidence of being richer in phytoplankton species than lakes in temperate zones. In fact, the reverse may even be true, as the Chrysophyceae are rare or absent in many tropical lakes (Lewis 1978a, 1979), while the diversity of other divisions may be similar to that in temperate systems. It has also been noted that Chrysophyceaen diversity and abundance is greatly reduced in some Florida lakes (Bienert 1983, and personal communication). Unfortunately, few tropical or subtropical algal data are available in enough detail to determine availabilities of dominant species to herbivores and particularly to species of the genus Daphnia.

A combination of factors then may be responsible for tropical and subtropical reductions in daphnid diversity. Certainly predation will influence the body-size structure of a zooplankton community in any given lake or set of lakes. When vertebrate predators (fish) dominate a lake, the zooplankton will consist of small body-sized individuals (Brooks and Dodson 1965), while large body-sized zooplankton should dominate a lake where vertebrate predators are absent (Brooks and Dodson 1965; Dodson 1974; Hall et al. 1976). Yet, the apparently universal reduction of daphnid species diversity in the tropics may not be due entirely to predation. Rather daphnid distributions may be determined by a combination of predation, temperature, and food quality or abundance.

The manner in which zooplankton partition resources may have a profound effect on the species diversity of a community; yet, the pelagic zone of freshwater habitats has been considered relatively uncomplex (Zaret 1975; Hall et al. 1976), thus there may be few ways in which zooplankton are able to partition niches. Segregation by habitat (vertical migration and vertical layering), by feeding times, and by food types may facilitate coexistence of several zooplankton species (Lane 1975; Hall et al. 1976), yet, may not be sufficient to explain how many similar zooplankton species are able to coexist in the pelagic of temperate lakes (Hutchinson 1961; Hall et al. 1976). In temperate systems, coexistence of similar phytoplankton and zooplankton species may actually be enhanced by the short periods of time that exist between environmental fluctuations (Hutchinson 1961). If the generation time of many species is approximately as long as the duration between environmental changes, exclusion of competitively inferior by competitively superior ones is abated (Hutchinson 1961). It may be predicted, then, that in a more constant environment, competitive exclusion of inferior species would occur, resulting in significant decreases in species diversity.

Subtropical and tropical aquatic habitats may supply just this constancy. Lake Lanao (Lewis 1978a, 1979) and Lake Victoria (Moss

1980) are classic examples, with water column temperatures ranging between 24° and 28°C throughout the year. In some Florida lakes (Brezonik et al. 1980; Crisman et al. 1982), temperatures for eight months of the year (October—May) span a 12-degree range (12—24°C) and fluctuate by only two or four degrees within any month. By contrast, the epilimnetic temperatures in north temperate lakes (Wetzel 1975) may fluctuate by as much as 20 degrees within a three-month period and as much as 10 degrees within a month. Therefore, the influence of environmental (temperature) stability on the nature of competitive interactions in the zooplankton and on species diversity in aquatic systems will be examined in this work.

Many ecologists have suggested that, as environmental variability decreases, species should become more specialized, niches should become narrower, tolerance for increased species packing should occur, and an overall increase in species diversity should be observed (May and MacArthur 1972; Abrams 1975; MacArthur 1976; McMurtrie 1976). However, Huston (1979) has shown that the relationship between environmental variability and species diversity is more complex. Assuming a certain level of environmental variability implies a certain rate of density independent disturbance, he suggests the following relationships. At constant population growth rates, a high rate of disturbance will decrease diversity due to frequent extinctions of some populations or species. Low to moderate rates of disturbance keep competing populations away from the carrying capacity (K) and increase diversity, while very low rates of disturbance decrease diversity due to competitive exclusion of some species near K. This hypothesis contrasts with the compression hypothesis (Schoener 1974) stated earlier, but both are compatible if habitat structural complexity is added as another variable in determining species diversity. Niche partitioning may be facilitated and species diversity increased when disturbance rates are very low in structurally complex environments (see Menge and Sutherland 1976 for a similar view). In simple environments, however, species packing may not be allowed; thus species diversity will be decreased (after Huston 1979).

Diversity may also depend upon the rates at which populations or species approach K (Huston 1979). Species that have low rates of increase may never have their competitive abilities tested if the rate of disturbance is moderate to high. If a rate of disturbance is faster than the rate of growth of populations (or species) that allows them to approach or reach K, then diversity will be increased due to a limitation of competitive interactions. If, on the other hand, the rate of disturbance is slower than the rate of growth that allows populations to reach K, then competitive exclusion or niche compression may occur (depending again on the degree of structural heterogeneity), and species diversity may be decreased or increased respectively.

If environmental fluctuations act as a disturbance that enhances species diversity by inhibiting competitive domination by one species in structurally homogeneous aquatic environments, then zooplankton species diversity should be higher in temperate aquatic habitats than in tropical ones if fluctuations or rates of fluctuation are higher in temperate habitats than in subtropical or tropical habitats. This is not an unfounded idea. Several workers have examined systems where disturbances have enhanced species diversity. Predation seems to be the most common mechanism of disturbance (Connel 1961; Harper 1969; Porter 1974; Neill 1975; Kerfoot and Pastorok 1978). Selective predation can maintain a relatively high local diversity by keeping species below K (Menge and Sutherland 1976). For example, a competitively superior organism may be held in check by a predator, allowing subordinate competitors to inhabit a system where they would normally be excluded in the absence of the predator. However, high rates of predation in structurally simple environments may also decrease species diversity due to overexploitation. Physical factors have also been shown to be important in maintaining species diversity in several studies (Dayton 1975; Levin and Paine 1974; Weins 1977), and it is the influence of these disturbances, or the lack of them, on species diversity that will be examined here.

In this work, I posit that reduced daphnid diversity in subtropical and tropical freshwater habitats is the result of competitive interactions between zooplankton species. These interactions may be enhanced by a relatively stable climatic setting where the time for competitive exclusion may be greater than in temperate habitats. The hypothesis tested here then is that competition is a mechanism by which certain daphnid species are excluded from structurally homogeneous, physically constant environments. The results of the tests of this hypothesis are combined with evidence favoring temperature and food resource stability in temperate and tropical aquatic systems in order to compare the tolerance of these systems for increased or decreased species diversity.

## Description of Study Site

King Pond, located in Gainesville, Florida (R19E, T9S), is a shallow (maximum depth 1.5 m), colored, unproductive pond with a surface area of ca. 0.5 ha. The pH of the pond water was ca. 7.0, total alkalinity was less than 15.0 µg/L, and chlorophyll-*a* concentrations ranged from 2.0 to 5.0 µg/L during the sampling period. King Pond was thermally stratified from April through September 1983, with maximum surface temperatures reaching 29°C (Figure 1). Oxygen concentrations in the pond were consistently low, with percent saturation values ranging from 6 to 95% during the sampling period (Figure 2).

*Daphnia laevis* is the only abundant cladoceran in King Pond. The occurrence of other cladoceran taxa (Table 1) is rare, while densities of *D. laevis* range from fewer than 5 organisms/L to over 300 organisms/L (juveniles + adults) (Figure 3). Maximum densities of *D. laevis* occurred in November—December and from April to August during this study.

The density of *Chaoborus* sp. also reached its maximum during the summer months (Figure 4). Periodic gut content analyses of *Chaoborus* were inconclusive, with only rotifers being found in gut samples.

Copepod nauplii were relatively abundant in King Pond in November—December, but dropped to very low levels during the rest of the sampling period (Figure 5). *Diaptomus floridanus* was abundant throughout the sampling period, while unidentified species of *Cyclops* and *Tropocyclops* occurred very infrequently (Figure 6). Rotifers (Table 1) were abundant only during November 1982 (Figure 6).

Six algal species were identified in King Pond during the sampling period. All species, including the four dominants (those that composed greater than 5% of total algal abundance at a sampling date), were unicellular, and their longest axes were all less than 15 μm in length (Figure 7 and 8, Table 2).

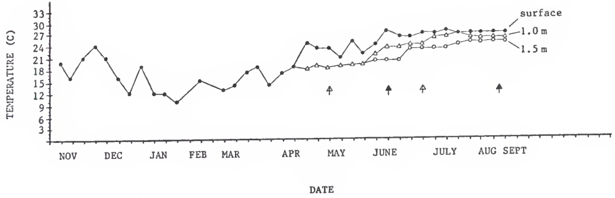


Figure 1. Water temperature in King Pond from November 1982 to September 1983. Where one line is used (Nov. to Apr.), temperature is for the entire water column. Open and closed arrows indicate the beginning and end of pond competition experiments respectively.

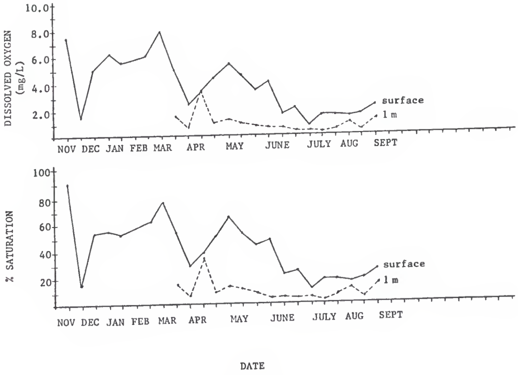


Figure 2. Dissolved oxygen concentration and percent saturation of dissolved oxygen in King Pond from November 1982 to September 1983. Where one line is used (Nov. to Apr.), values are for the entire water column.

Table 1. Zooplankton taxa collected in King Pond from November 1982 to September 1983.

Arthropoda

- Crustacea
    - Cladocera
        - *Daphnia laevis*
        - *Diaphanosoma brachyurum*
        - *Eubosmina* sp.
        - *Latonopsis occidentalis*
        - *Simocephalus serrulatus*
    - Copepoda
        - *Tropocyclops* sp.
        - *Cyclops* sp.
        - *Diaptomus floridanus*

Rotifera

- Monogonata
    - Ploima
        - *Brachionus havanaensis*
        - *B. calyciflorus*
        - *Euchlanis* sp.
        - *Keratella* sp.
        - *Lecane* sp.
        - *Monostyla* sp.
        - *Synchaeta* sp.
        - *Trichocerca similis*
    - Flosculariacea
        - *Testudinella parva*

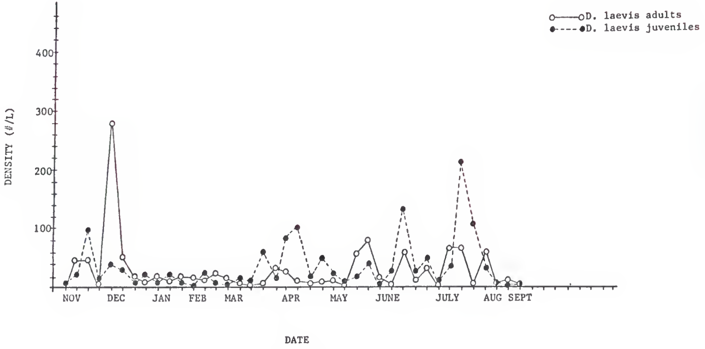


Figure 3. Densities of Daphnia laevis juveniles and adults in King Pond from November 1982 to September 1983.

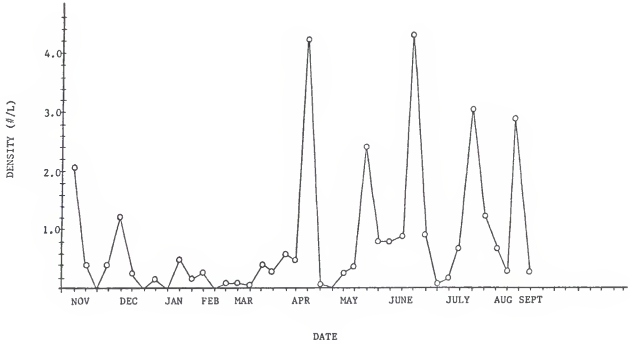


Figure 4. Densities of Chaoborus sp. in King Pond from November 1982 to September 1983.

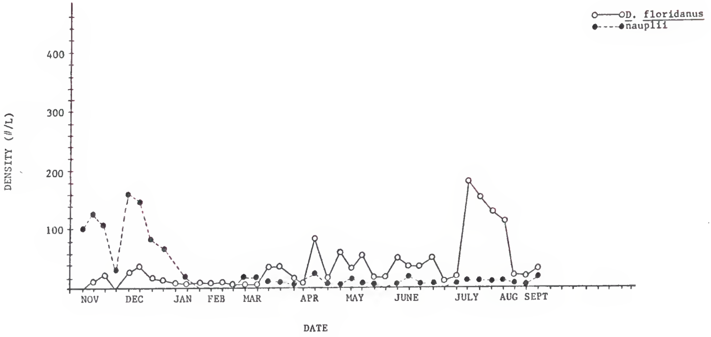


Figure 5. Densities of Diaptomus floridanus (copepodids and adults), and densities of copepod nauplii in King Pond from November 1982 to September 1983.

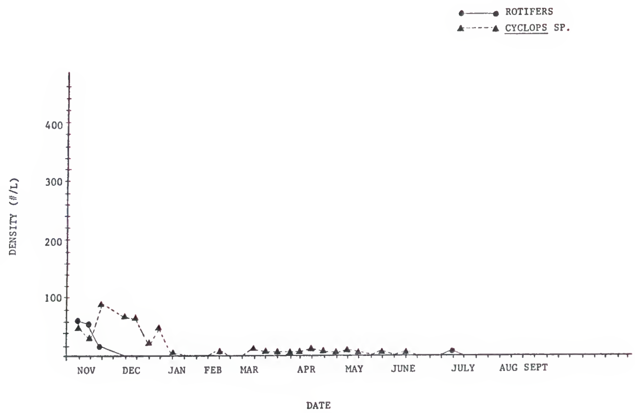


Figure 6. Densities of Cyclops sp. (copepodids and adults), and the density of rotifers in King Pond from November 1982 to September 1983.

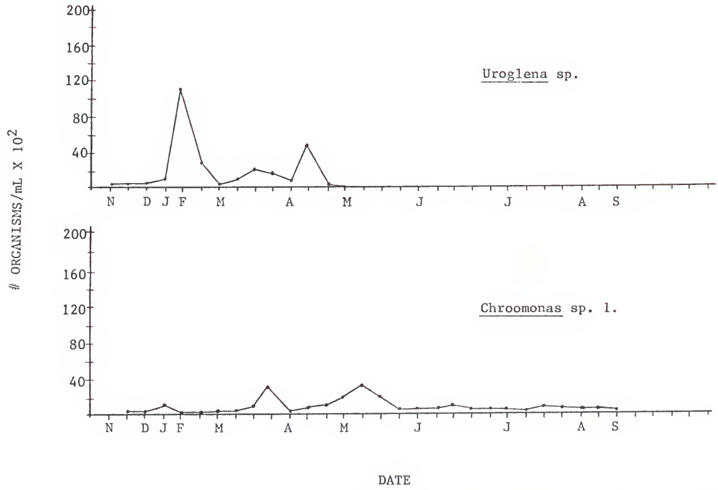


Figure 7. Densities of dominant algal species in King Pond from November 1982 to September 1983.

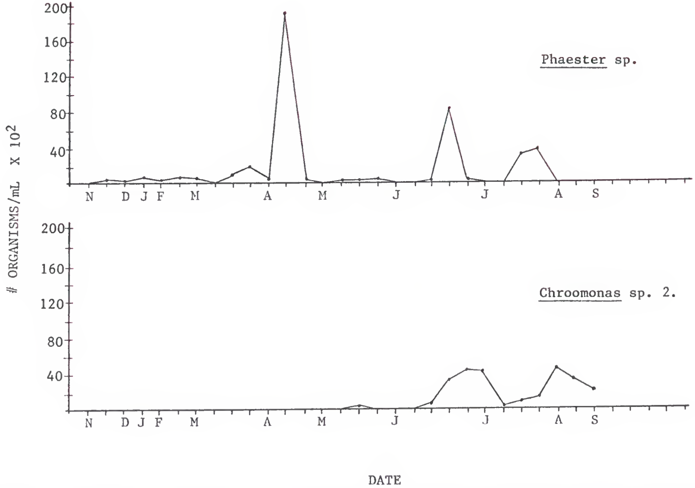


Figure 8. Densities of dominant algal species in King Pond from November 1982 to September 1983.

Table 2. Algal taxa collected in King Pond from November 1982 to September 1983. * denotes species comprising greater than 5% of the total algal abundance on any sampling date.

Chlorophyta

- *Mougeotia* sp.

Cyanophyta

- *Anabaena* sp.

Cryptophyta

- *Chroomonas* sp. 1
- *Chroomonas* sp. 2
- *Cryptomonas ovata*
- *Phaester* sp.
- *Uroglena* sp.
- *Chrysoamoeba* type

Bacillariophyta

- unidentified frustules

# CHAPTER 2
# MATERIALS AND METHODS

Zooplankton in King Pond were collected weekly or biweekly from November 1982 to October 1983 at one central station. Prior to November, I collected replicate zooplankton samples several times at two stations in the pond and determined that there were no differences between the number and types of species at either station. For this reason, and due to the small surface area of the pond (less than 1 ha), I chose one central location at which I completed all analyses.

Zooplankton were collected by filtering a 6.6-L water sample, collected with a clear 2.2-L Kemmerer water bottle through a #20 (80 μm) Wisconsin style plankton net. Material retained by the filter was preserved with 5% sugar-formalin solution (Haney and Hall 1973). Phytoplankton samples were collected weekly or biweekly from whole water samples and preserved with a 1% Lugols solution. Temperature and dissolved oxygen data were collected with a YSI model 56 dissolved oxygen-temperature meter at each sampling date. pH, alkalinity, secchi disk depths and chlorophyll samples were measured or taken periodically throughout the sampling period. pH was measured with a Beckman Zeromatic II pH meter. Total alkalinity was measured using standard titration techniques (APHA 1980).

In the laboratory, chlorophyll concentrations were determined spectrophotometrically according to the trichromatic method (APHA

1980). Phytoplankton were identified and enumerated by settling subsamples in Utermohl chambers and analyzing subsamples with a Leitz Diavert inverted microscope at 450 or 1000 X magnification. Zooplankto were analyzed by extracting duplicate, 1-mL subsamples from preserved samples and placing them in a chambered counting cell (Gannon 1971), where zooplankton were identified and enumerated at 100 X magnification with a Leitz compound microscope. Due to relatively low concentrations of cladocera in King Pond, zooplankton were also analyzed by extracting duplicate 10-mL subsamples that were placed in a counting wheel and analyzed with an American Optical binocular dissecting microscope at 40 X magnification. This method allowed me to obtain cladoceran numbers (eggs, juveniles, and adults) large enough for statistical evaluation.

## Laboratory Experiments

Laboratory cultures of Daphnia magna Straus were initiated with individuals obtained from the Environmental Protection Agency, Duluth, Minnesota. Laboratory cultures of Daphnia laevis Birge were initiated from organisms obtained from King Pond on 15 January 1982. All animals were cultured in aged (2 weeks) tap water at 21°C with a 12:12 light-dark cycle (40 watt cool-white fluorescent light). Animals were fed suspensions of Chlamydomonas reinhardi Dangeard in log growth phase either daily, when large populations were needed for competition studies, or every other day. C. reinhardi, obtained from the Starr collection at the University of Texas and cultured in autoclaved Woods Hole MBL medium at 21°C, is an excellent and widely accepted alga for use in zooplankton cultures and experiments (Porter and Orcutt 1980; Goulden et al. 1982a).

Life history data were determined for D. laevis and D. magna individuals as follows: five newborn (day 0) animals were obtained from the brood of a parthenogenic female and placed in a beaker with aged tap water and measured concentrations of C. reinhardi. All parthenogenic females were acclimated to experimental conditions at least 7 days prior to use of their offspring in experiments. This process was triplicated for each species using offspring from different individual females for each replicate, and run at two algal concentrations ($1 \times 10^4$ and $5 \times 10^5$ cells/mL) and three temperatures (15°, 21°, and 27°C). Animals from each beaker were removed, enumerated, and placed in new medium daily. There is evidence that after day 21, any reproduction has no significant influence on the intrinsic rate of population growth, $r_m$ (Goulden et al. 1982a); therefore, experiments were continued until all animals of the original cohort had died or until day 21 of the experiment. All newborn individuals in a beaker were also enumerated and discarded, and the length of shed carapaces of adults was measured after each reproduction. To obviate rapid food (algal) depletion due to differential grazing of large and small daphnid species (Burns 1969), I utilized a method similar to that used by Goulden et al. (1982b), where the life history characteristics of D. magna were measured in 300 mL of medium, and those of D. laevis were measured in 100 mL of medium.

The rate of population growth, $r_m$, was obtained from the equation

$$1 = \sum_{x=0}^{\infty} e^{-r_m x} \ell(x) m(x)$$

where $\ell(x)$ is the proportion of newborn individuals surviving to age x, and $m(x)$ is the age specific fecundity rate. I also determined $q(x)$, the age specific death rate, $p(x)$, age specific survivorship, $d(x)$, the proportion of newborn dying between age x and age x + 1, and $v(x)$, the reproductive value of an x-year old.

Competitive interactions between *D. magna* and *D. laevis* were examined in the laboratory in 2000 mL of aged tap water at 15°, 21°, and 27°C. Experiments included examination of interactions between the following combinations of the two species:

10 *D. laevis* juveniles and 10 *D. magna* juveniles
10 *D. laevis* juveniles and 10 *D. magna* adults
10 *D. laevis* adults and 10 *D. magna* juveniles
20 *D. laevis* juveniles
20 *D. magna* juveniles

Food (*C. reinhardi*) was initially introduced at a concentration of 1 x $10^4$ cells/mL. *C. reinhardi* concentrations were measured every four days in all beakers at 21°C by extracting 10 mL of water from a beaker, preserving with 1% Lugols, and placing 1 mL in a Sedgwick-Rafter chamber where the number of cells/mL was determined microscopically. Cell concentrations were restored to 1 x $10^4$ cells/mL in all beakers every four days.

In one set of interactions (10 *D. laevis* and 10 *D. magna* juveniles, 21°C), algal concentrations were measured daily as above, from day 4 to day 8, days 16 to 20, 20 to 24, 28 to 32, and 32 to 36. This allowed an examination of the rate of algal depletion at various daphnid population sizes. I also monitored bacteria concentrations infrequently in competition jars at 21°C. Bacteria were concentrated from whole water samples on 0.45 µm Millipore® filters and fixed and enumerated using the techniques of Hobbie et al. (1977).

As laboratory competition experiments were begun at 21°C, I used different sampling regimes at this temperature to determine an ideal period between sampling dates. I used an 8-day frequency in one competition experiment, and an initial 2-week, then 10-day frequency in another competition experiment. The outcome of both experiments was similar, so I chose the 8-day sampling frequency for all other experiments, as this period allowed greater delineation of impacts of competitive interactions on daphnid population dynamics during an experiment.

Generally, at 8-day intervals, cell concentrations were determined as above, then all animals were carefully removed with a widemouth pipette, enumerated (juveniles and adults), and placed in clean jars with new water and $1 \times 10^4$ cell/mL *C. reinhardi*. Animals that were larger than the minimum size of egg-bearing females (determined in life history experiments) were considered to be adults. All experiments were continued until the complete exclusion of one species occurred.

## Field Experiments

Small, 300-mL opaque plastic bottles capped with 153 m Nitex nylon were used to evaluate competitive interactions between *D. magna* and *D. laevis* in King Pond. All bottles were filled with filtered (153 µm) pond water and the following combinations of *D. magna* and *D.*

*laevis* (both taken from temperature-acclimated laboratory cultures) introduced:

5 *D. magna* juveniles and 5 *D. laevis* juveniles
2 *D. magna* juveniles and 2 *D. laevis* juveniles
10 *D. magna* juveniles and 10 *D. laevis* juveniles
5 or 2 *D. magna*, or 5 or 2 *D. laevis* juveniles at 21°C
2 *D. magna* or 2 *D. laevis* juveniles at 15° and 27°C.

All experimental manipulations were triplicated. Bottles were placed in a cage and suspended in the pond, usually at 0.5 m depth. All bottles were removed every three days, animals removed and enumerated as in laboratory competition studies, then placed in clean jars with fresh filtered water and resuspended in the pond. All experiments were run until the complete exclusion of one species occurred.

The availability of food in small enclosures is dependent upon the amount of flow or water exchange across the Nitex cap. I checked water exchange by introducing a dye (crystal violet) into bottles filled with water and measuring dye concentrations spectrophotometrically. Bottles were placed in the pond at 0.5 m depth and dye concentrations were measured after 24, 48, and 72 hours. A control bottle with crystal violet stained water and standard cap that did not allow any water exchange was also placed at 0.5 m depth and dye concentrations measured initially and after 72 hours. Since dye concentrations did not change in any bottle (including the control) during the experiment, it was determined that flow across the Nitex cap was minimal; thus organisms in experimental and control bottles were enumerated (juveniles and adults) and tranferred to clean bottles every three days. Experiments were run from February 1983 to September 1983. However, successful introductions were made only after April 1983 (Figure 1).

Field and laboratory competition experiments are, of course, miniaturized, artificial replications of real or portions of real ecosystems. Thus some random events occurred (e.g., death of all animals shortly after introduction) that are likely unrelated to real phenomena and have no bearing on the conclusions drawn in this study. If these random events seemed at all pertinent, they were included in the analysis; otherwise, they were not. All replicated laboratory competition experiments are reported. I did not replicate laboratory competition experiments that were begun with adult-juvenile combinations. Results of duplicated laboratory controls (single species) were remarkably similar; thus I have generally reported only the outcome of one control at each temperature. The outcome of field experiments was sometimes tenuous, and I have done my best to include all data that seemed even remotely pertinent. In fact, approximately 30% of all attempts to begin competition or control experiments were unsuccessful, that is, all organisms only lived for short periods of time after introduction; thus these data are generally not included in the analysis. All competition and control experiments were at least triplicated, and I have reported here the outcome of all reasonably successful field experiments.

All analyses that required the use of a computer (life history, statistics, etc.), were performed on the University of Florida's (Northeast Regional Data Center) IBM 3081 computer.

# CHAPTER 3
# RESULTS AND DISCUSSION

I collected and compared life history and demographic data for *Daphnia laevis* and *Daphnia magna* to determine the effects of three temperatures and high and low food (*C. reinhardi*) concentrations on various fitness parameters of the two species. Analysis of variance showed that both temperature and food concentration have significant effects on the intrinsic rate of population growth of both species (Table 3). There is also a significant interaction effect between food and temperature on $r_m$, which suggests that responses of $r_m$ to variation in food concentrations and temperature are not uniform over the various levels of treatment.

Temperature and food concentration also have significant effects on the age of first reproduction in both species, but there is significant interaction between the two factors only in *D. magna* (Table 3). The size of the first reproduction (fecundity) is only affected by food concentration in both species, and there is no significant interaction between food and temperature for this variable (Table 3). The age at first reproduction and the size of the first brood are the two components that have the greatest influence on the intrinsic rate of population growth, $r_m$ (Lynch 1980) and are therefore used, along with $r_m$, for further comparisons of the effects of food concentration and temperature on fitness components of *D. magna* and *D. laevis*.

Table 3. Analysis (ANOVA) of the effects of food (algal) concentrations and temperature on $r_m$, the age at first reproduction, and fecundity at first reproduction of *D. magna* and *D. laevis*.

| *Daphnia magna* | DF | F | SIGNIFICANCE (p = 0.01) |
|---|---|---|---|
| Source of variation in $r_m$ | | | |
| FOOD | 1 | 501.3 | * |
| TEMPERATURE | 2 | 92.2 | * |
| INTERACTION | 1 | 41.6 | * |
| Source of variation in age at first reproduction | | | |
| FOOD | 1 | 43.4 | * |
| TEMPERATURE | 2 | 116.1 | * |
| INTERACTION | 1 | 5.9 | * |
| Source of variation in fecundity at first reproduction | | | |
| FOOD | 1 | 15.6 | * |
| TEMPERATURE | 2 | 0.2 | NS |
| INTERACTION | 1 | 0.5 | NS |

| *Daphnia laevis* | DF | F | SIGNIFICANCE (p = 0.01) |
|---|---|---|---|
| Source of variation in $r_m$ | | | |
| FOOD | 1 | 159.3 | * |
| TEMPERATURE | 2 | 58.3 | * |
| INTERACTION | 1 | 18.4 | * |
| Source of variation in age at first reproduction | | | |
| FOOD | 1 | 5.4 | * |
| TEMPERATURE | 2 | 188.3 | * |
| INTERACTION | 1 | 2.2 | NS |
| Source of variation in fecundity at first reproduction | | | |
| FOOD | 1 | 54.5 | * |
| TEMPERATURE | 2 | 0.4 | NS |
| INTERACTION | 1 | 3.8 | NS |

There is a significant increase in $r_m$ with temperature at high food concentrations in both species (Figures 9 and 10). Comparison between species shows that, at 15°C (high food), there is no significant difference between $r_m$ of _D. magna_ and _D. laevis_, but at 21° and 27°C, _D. laevis_ has a significantly higher $r_m$ (Table 4). These values compare well with other literature values for both species. At 20°C and at food concentrations of less than $1 \times 10^4$ cells/mL, $r_m$ for _D. magna_ ranges from 0.10 to 0.32 ($\text{day}^{-1}$), while at 20°C and at food concentrations of greater than $1 \times 10^4$ cells/mL, $r_m$ for _D. magna_ ranges from 0.28 to 0.38 ($\text{day}^{-1}$) (Goulden et al. 1982b; Porter et al. 1983). The only value of $r_m$ available for _D. laevis_ (at 25°C and at undetermined food concentrations) is 0.55 (Lynch 1980), which again falls within the range of values found in my study.

Changes in $r_m$ may be explained by the age and brood size at first reproduction in both species. The age at first reproduction decreases with increasing temperature for both _D. magna_ and _D. laevis_ (Figures 9 and 10, Table 4); however, the brood size at first reproduction does not change with changing temperature for either species. In all cases at a given temperature, _D. laevis_ has a significantly earlier age at first reproduction than does _D. magna_. However, only at 15°C does one species (_D. laevis_) have a significantly larger brood at first reproduction. It appears then that _D. laevis_ realizes its higher intrinsic rate of population growth by beginning reproduction at an earlier age than _D. magna_. This is true only at 21° and 27°C, however, which is due to the fact that even though _D. laevis_ has a larger first brood than _D. magna_ at 15°C, both species begin reproduction at older

Figure 9. The intrinsic rate of population growth ($r_m$), the age at first reproduction, and the average brood size at first reproduction of *Daphnia magna* expressed as a function of temperature, and high (HF = $5 \times 10^5$ cells/mL *Chlamydomonas reinhardi*) or low (LF = $1 \times 10^4$ cells/mL *C. reinhardi*) food concentrations. Points without error bars have standard deviations of 0. N = 3 experimantal replications for each point.

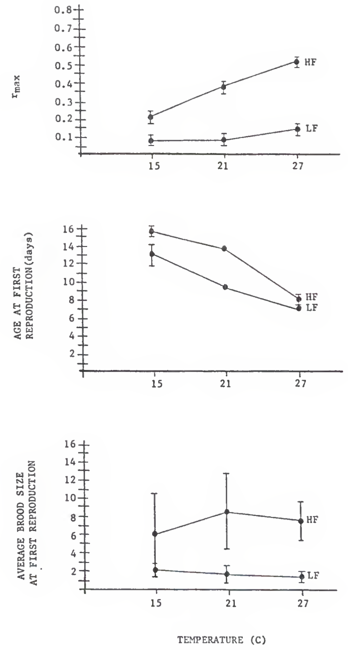

$r_{max}$
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
HF
LF
15
21
27
AGE AT FIRST REPRODUCTION (days)
16
14
12
10
8
6
4
2
HF
LF
15
21
27
AVERAGE BROOD SIZE AT FIRST REPRODUCTION
16
14
12
10
8
6
4
2
HF
LF
15
21
27
TEMPERATURE (C)

Figure 10. The intrinsic rate of population growth ($r_m$), the age at first reproduction, and the average brood size at first reproduction of D. laevis expressed as a function of temperature and high or low food concentrations (as in Figure 9). Points without error bars have standard deviations of 0. N = 3 experimental replications for each point.

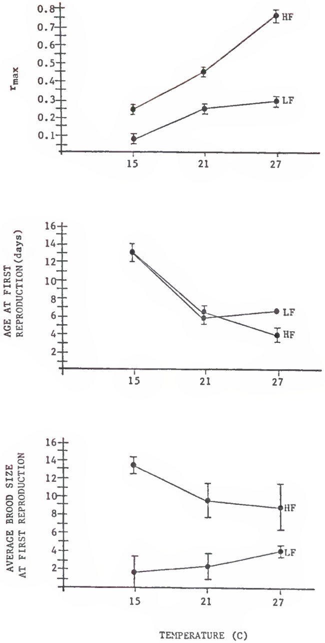

r_max
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
HF
LF
15
21
27
AGE AT FIRST REPRODUCTION (days)
16
14
12
10
8
6
4
2
LF
HF
15
21
27
AVERAGE BROOD SIZE AT FIRST REPRODUCTION
16
14
12
10
8
6
4
2
HF
LF
15
21
27
TEMPERATURE (C)

Table 4. $r_m$, the age at first reproduction, and fecundity at first reproduction of *D. magna* and *D. laevis* at high and low food (algal) levels and at three temperatures. Values sharing letters are not significantly different from each other ($p>0.05$). Statistical differences measured with a Duncan's multiple range test.

*Daphnia magna*

| | HIGH FOOD | | | LOW FOOD | | |
|---|---|---|---|---|---|---|
| | 15°C | 21°C | 27°C | 15°C | 21°C | 27°C |
| $r_m$ | 0.215ao | 0.370b | 0.528c | 0.086d | 0.082d | 0.138e |
| age @ first reproduction | 14.7f | 9.0g | 6.3hs | 16.0L | 14.0f | 8.0iw |
| average fecundity @ first reproduction | 5.7jkv | 8.5ky | 7.4jk | 2.0jv | 1.5jv | 1.4jv |

*Daphnia laevis*

| | HIGH FOOD | | | LOW FOOD | | |
|---|---|---|---|---|---|---|
| | 15°C | 21°C | 27°C | 15°C | 21°C | 27°C |
| $r_m$ | 0.235ao | 0.468p | 0.783q | 0.077d | 0.246ao | 0.307o,b |
| age @ first reproduction | 12.0rf | 6.3sh | 4.3t | 13.0f | 7.0shw | 6.0sh |
| average fecundity @ first reproduction | 12.5uy | 9.2uk | 8.8uk | 1.7v | 2.5v | 4.3v |

ages than at other temperatures, thus losing the advantage accrued by reproducing early.

An example serves to make these points clearer. At 15°C, if the age of first reproduction for D. magna is decreased from 15 to 10 days (a decrease easily realized, Table 4) without any change in brood size, the intrinsic rate of population growth would increase from 0.21 to 0.31. Fecundity at first reproduction would have to be 14 times higher than that realized at 15°C by D. magna to match the effects of a 5-day decrease in the age of first reproduction on $r_m$. This would require that the average individual female produce 80 offspring at first reproduction, a brood size that is approximately 10 times higher than the highest fecundity at first reproduction for D. magna at any temperature. Changes in fecundity at later ages have relatively little effect on $r_m$ regardless of their magnitude.

Fitness components associated with $r_m$ have, in the past, been compared with competitive abilities through the theory of r-K selection (Pianka 1970, 1972, 1978; Stearns 1976). Organisms that have evolved under the influence of density-independent selective pressures that favor rapid development, high $r_m$, early reproduction and small body size (r-selection) are thought of as being inferior competitors to organisms that have evolved under the influence of density-dependent selective pressures that favor slower development, delayed reproduction, fewer, larger progeny, and larger body size (K-selection). If this, in fact, is true, then D. magna should be a superior competitor when compared to D. laevis, once populations reach some carrying capacity where conditions become limiting.

Demographic traits at low or limited food concentrations should reflect characteristics of a species that are realized when populations are near the carrying capacity in an environment. "K-selected" species should generally fare better (have a higher rate of population growth) near the carrying capacity, than species (or genotypes) selected for maximal population growth away from K, in this case under conditions where food is abundant. Therefore, I compared the demographic characteristics of the two species under limited food concentrations (1 x $10^4$ cells/mL, 0.2 mg C/L, Lampert 1978; Porter et al. 1982) at three temperatures to test this phenomenon. I then used these results to predict competitive success and tested these predictions by examining the outcome of interspecific competition between D. laevis and D. magna under limited food concentrations at three temperatures.

At low food concentrations (1 x $10^4$ cells/mL), D. laevis has a significantly higher intrinsic rate of population growth ($r_m$) than D. magna at 21° and 27°C, while there is no significant difference between $r_m$ of the two species at 15°C (Table 4). The differences at 21° and 27°C are apparently accounted for by the fact that D. laevis begins reproduction at an earlier age than D. magna. There are no significant differences in first brood size between the species. At 15°C, D. laevis begins reproduction earier than D. magna, but both species begin reproducing relatively late in life (as they do at 15°C, high food), thus again losing any advantage of increasing $r_m$ by beginning reproduction at an early age.

From life history data calculated at low food levels, I predict that D. laevis should be a superior competitor compared to D. magna at 21° and 27°C. Neither animal has a fitness (reproductive component) advantage at 15°C and the result of competition between the two species is not predictable at this temperature.

Laboratory competition experiments show that, indeed, *D. laevis* is the superior competitor at 21° and 27°C (Figures 11 and 12). Competition here results not just in suppression of one population by another (as in Goulden et al. 1982b and Cooper and Smith 1982), but in complete exclusion of *D. magna* from competition jars. At 21°C, *D. laevis* outcompetes *D. magna* regardless of adult-juvenile ratios at the beginning of an experiment (Figure 13) although there is some initial suppression of *D. laevis* populations (within the first 15—20 days) when *D. magna* adults are used to initiate a competition experiment. Exclusion of *D. magna* takes between 30 and 50 days at 21°C, while at 27°C exclusion occurs after 65 days (one competition experiment ended after 16 days with the death of both species [Figure 12] and is disregarded in this analysis). Controls show conclusively that both species can maintain their populations in the absence of the other, although *D. magna* control population densities are generally lower than *D. laevis* control populations (Figures 14 and 15).

At 15°C (Figure 16), *D. laevis* again outcompetes *D. magna* although this was not predicted from the life history analysis. Exclusion takes between 50 and 60 days at this temperature and occurs when *D. laevis* populations are at densities similar to those where exclusion occurs at 21° and 27°C. Peak *D. magna* populations (juveniles + adults) in competition jars at 15°C occur about 10 days later than at other temperatures, which is likely due to the greatly increased age at first reproduction of the species at 15°C. *D. laevis* peaks are also delayed, likely for similar reasons. Both species survive well in controls,

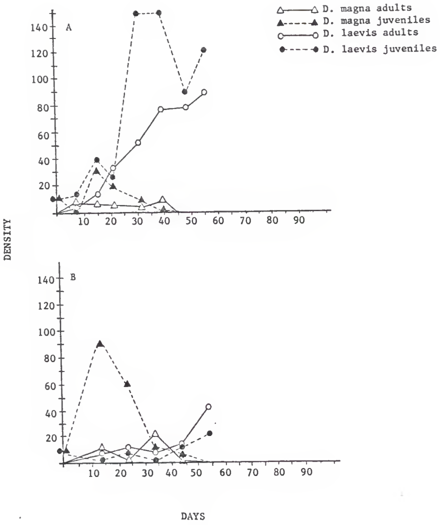


Figure 11. Population dynamics of Daphnia magna and D. laevis in replicate laboratory competition experiments at 21°C, with two sampling schedules - every eight days (A), or two weeks then every ten days (B). Density = total # organisms in 2L beaker.

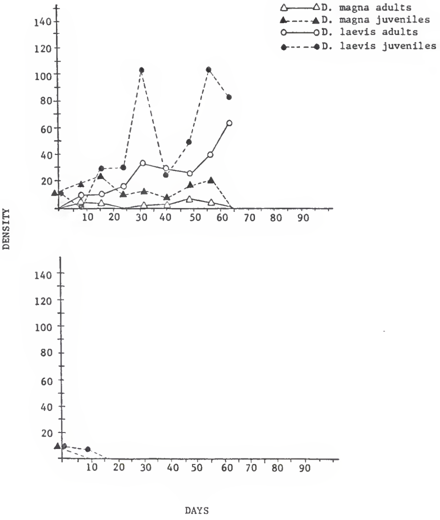


Figure 12. Population dynamics of Daphnia magna and D. laevis in replicate laboratory competition experiments at 27°C. Density = total # organisms in 2L beakers.

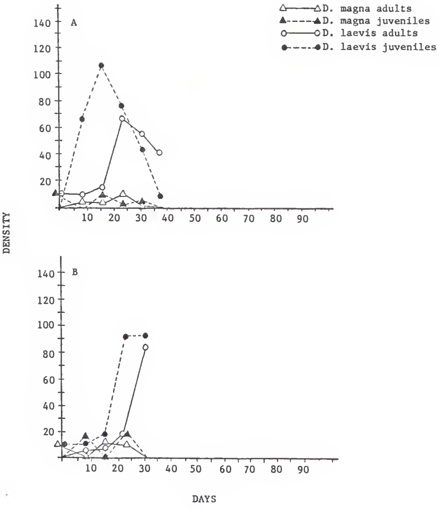


Figure 13. Population dynamics of Daphnia magna and D. laevis in laboratory competition experiments at 21°C, with starting densities of 10 D. magna juveniles and 10 D. laevis adults (A), or 10 D. magna adults and 10 D. laevis juveniles (B). Density = total # organisms in 2L beaker.

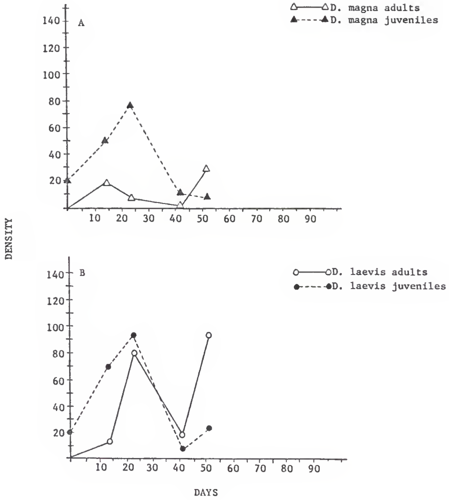


Figure 14. Population dynamics of Daphnia magna (A) or D. laevis (B) in laboratory control experiments at 21°C. Density = total # organisms in 2L beakers.

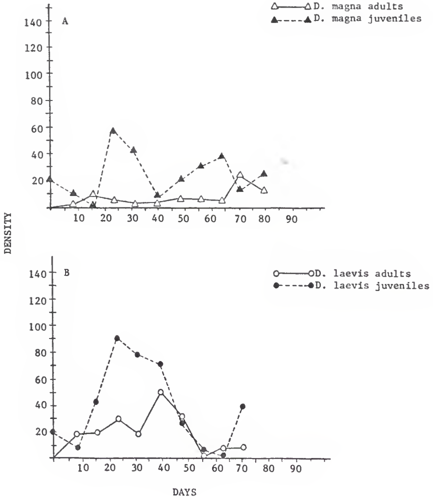


Figure 15. Population dynamics of Daphnia magna (A) or D. laevis (B) in laboratory control experiments at 27°C. Density = total # organisms in 2L beakers.

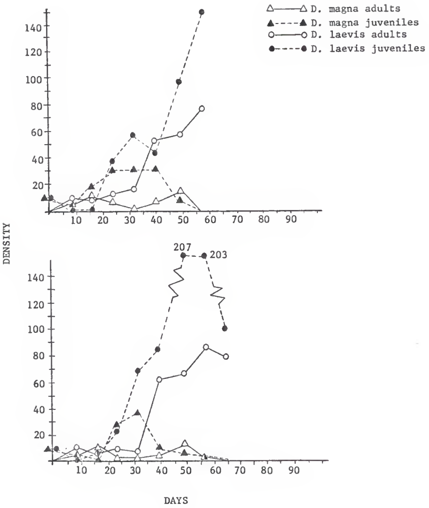


Figure 16. Population dynamics of Daphnia magna and D. laevis in replicate laboratory competition experiments at 15°C. Density = # organisms in 2L beakers.

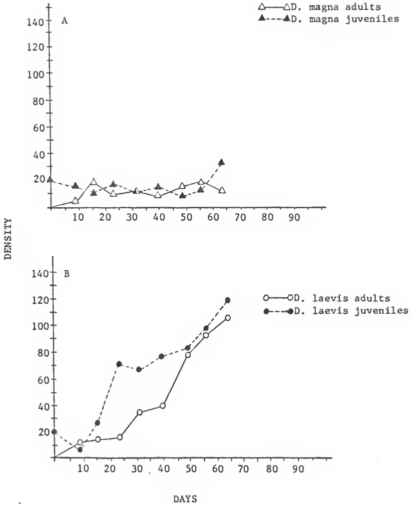


Figure 17. Population dynamics of Daphnia magna (A) or D. laevis (B) in laboratory control experiments at 15°C. Density = total # organisms in 2L beakers.

however *D. magna* populations equilibrate at much lower densities than *D. laevis* populations (Figure 17).

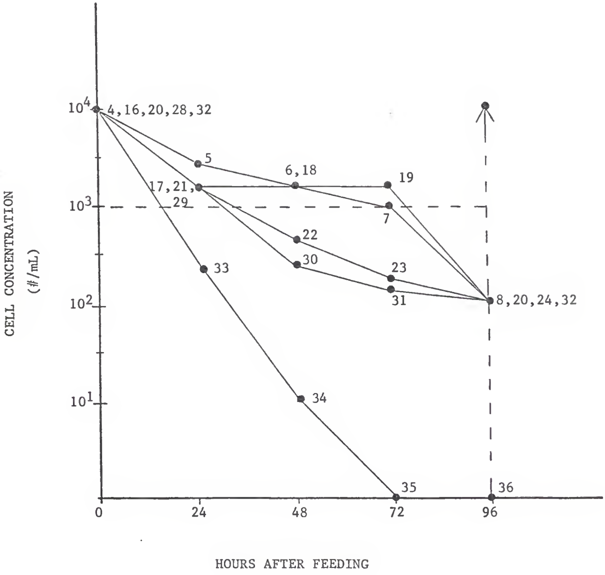
Generally, competitive suppression or exclusion of zooplankton is thought to occur via exploitative competition, that is, suppression of shared resources, but no definitive tests have been made to confirm the phenomenon in this study, or in others (Goulden et al. 1982b; Smith and Cooper 1982). In fact, control experiments in this study and others show that individual species can survive at low food concentrations and at relatively high population densities. Two possibilities exist to explain this phenomenon. 1) Intraspecific competition may not be nearly as important as interspecific competition in causing exclusion. This may be particularly true if competitive interactions occur between the adults of one species and the juveniles of another. However, this assumes that adult and juvenile individuals of one species are utilizing different sized resources, a possibility that does not exist in this work where only one algal species was supplied as a food source. 2) Interference competition may be the method that causes exclusion in these experiments.

There is little evidence for interference competition among zooplankton. Folt and Goldman (1981) suggest that the copepod *Epischura nevadensis* releases a compound that suppresses the filtering rate of the copepod *Diaptomus tyrelli*, and that this may be an example of interference competition between the two species. However, they also recognize that an increase in fitness may be accrued by *D. tyrelli* when it decreases its filtering rate in the presence of *Epischura* (or in the presence of a chemical released by *Epischura*), since *Epischura* is known to prey heavily on *D. tyrelli*.

As already stated, my results do not conclusively show that exploitative competition is the exclusive force at work in determining the outcome of competitive interactions between D. laevis and D. magna. A proper control may consist of an examination of interactions between the two species at nonlimiting food levels. If, as populations reach some critical density while food levels are kept high, one species is suppressed or excluded from a culture, then it is possible that interference between species is occurring. A further test, then, may be one similar to that employed by Folt and Goldman (1981) where water from a high density culture of one species is introduced into a culture of another potentially competing species.

I did examine the daily dynamics of food concentrations in one experimental situation (competition, limited food, 21°C, Figure 18), and it is obvious that food suppression is occurring in this competition beaker. In fact, food concentrations drop below what may be a level necessary to sustain metabolic requirements for some species (0.05 mg-C/L, Lampert 1977) after day 7 and remain consistently below 0.05 mg-C/L, even after food levels are replenished by day 21. It is noteworthy that, at 21°C, populations of D. magna are generally becoming suppressed in competition beakers by day 20 (Figure 11) and are generally excluded a relatively short time after this. D. laevis populations, however, continue to increase even after food levels drop to severely low concentrations (day 30, Figure 11). It is possible that D. laevis is better able to utilize other food sources (bacteria) when C. reinhardi reaches very low concentrations. Bacteria concentrations in laboratory competition enclosures ranged from $6.2 \times 10^5$ to $9.4 \times 10^5$ cells/L. Unfortunately, very little work has been performed on

Figure 18. Algal concentrations in competition beaker A (Figure 11) beginning 4 days after experiment was initiated, and monitored on days indicated (numbers by each point). Food (algal) levels were replenished to $1 \times 10^4$ cells/mL every 4 days (arrow). Horizontal dotted line is the lowest food concentration where *Daphnia* spp. are able to meet metabolic requirements (ca. $1 \times 10^3$ cells/mL, 0.05 mgC/L) after Lampert (1977). All statistical error about a point is less than one order of magnitude. $N = 5$ for each measurment.


CELL CONCENTRATION
(#/mL)
$10^4$
$10^3$
$10^2$
$10^1$
0
24
48
72
96
HOURS AFTER FEEDING
4,16,20,28,32
5
6,18
19
17,21,
29
7
22
30
23
31
33
34
35
36
8,20,24,32

differential utilization of bacteria by zooplankton. Daphnia species do have the ability to filter bacterial-sized particles (Gerritsen and Porter 1982), and there have been significant distinctions made between the filtering abilities of Bosmina and Daphnia fed both Chlamydomonas and bacteria (DeMott and Kerfoot 1982). However, bacterial particles of size less than 1 μm have been shown to be a poor source of nutrition for D. parvula (Pace et al. 1983). The implications of these data will be discussed later.

Pond competition studies show that D. laevis is clearly not a species whose dominance is limited to laboratory situations. At 21° and 27°C, D. laevis excludes D. magna from competition jars regardless of starting densities, but exclusion takes longer at 27°C than at 21°C, a phenomenon that was also observed in laboratory competition studies (Figures 19–22). Both species survive well in controls (Figures 23–26), but D. laevis populations in controls reach higher densities than D. magna populations at both temperatures. Unfortunately, competition experiments were never successful at temperatures near 15°C (animals did not survive in either competition or control jars). Animals were always acclimated to 15°C prior to introduction into King Pond, but it is likely that rapid, daily drops in temperature of greater than 5°C that occurred during this period were lethal to both species, especially when they were inhibited from normal vertical migratory behavior by confinement in enclosures.

Temperatures in King Pond were constant for several weeks once they reached 27°C, while there was some slight fluctuation about 21°C. This fluctuation was tempered slightly as experimental enclosures were suspended at 0.5 m depth, and temperatures at this depth were rela-

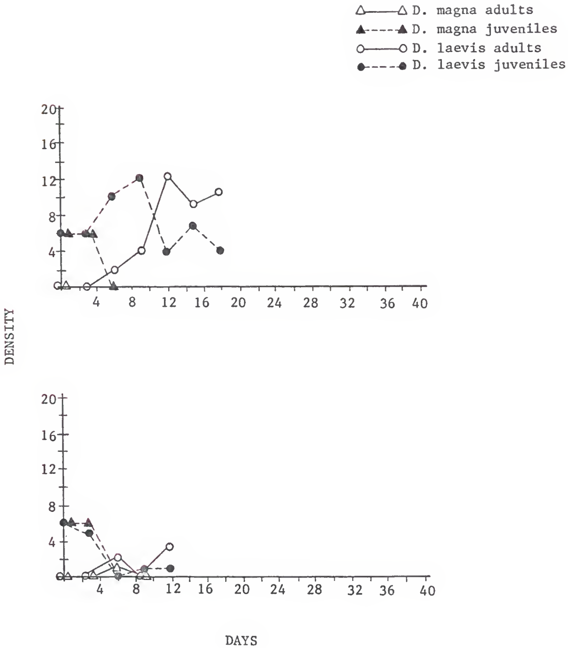


Figure 19. Population dynamics of Daphnia magna and D. laevis in King Pond competition experiments at 21°C. Density = total # organisms in 300mL enclosures.

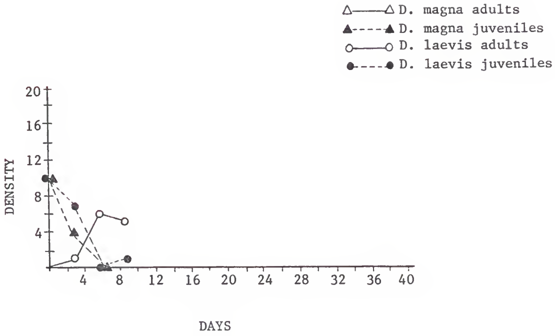
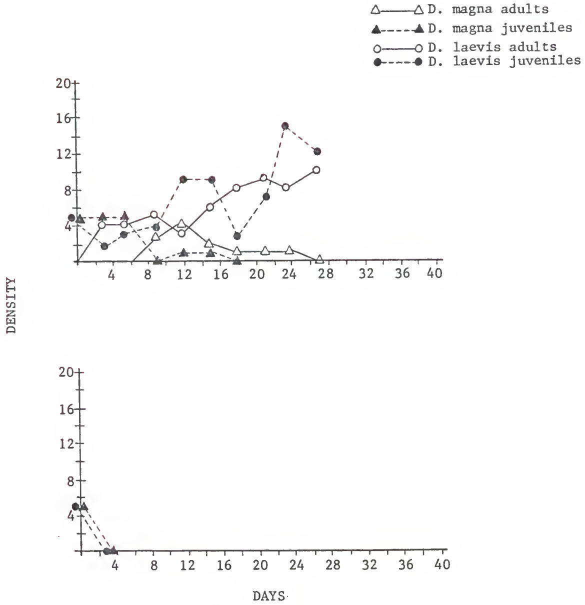


Figure 20. Population dynamics of Daphnia magna and D. laevis in King Pond competition experiments at 21°C, with starting densities of 10 juveniles of each species. Density = total # organisms in 300mL enclosures.



Figurs 21. Population dynamics of Daphnia magna and D. laevis in King Pond competition experiments at 27°C, with starting densities of 5 juveniles of each species. Density = total # organisms in 300mL enclosures.

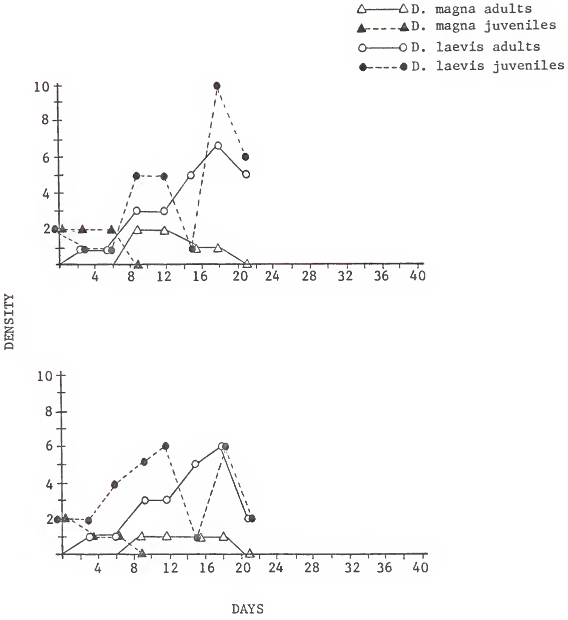


Figure 22. Population dynamics of Daphnia magna and D. laevis in King Pond competition experiments at 27°C, with starting densities of 2 juveniles of each species. Density = total # organisms in 300mL enclosures.

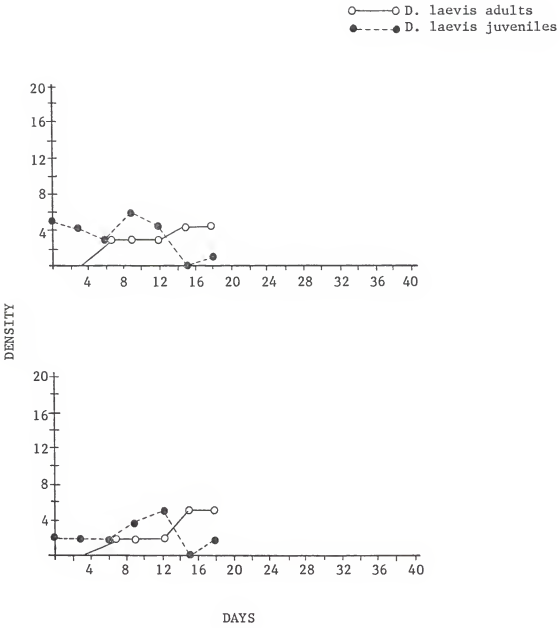


Figure 23. Population dynamics of Daphnia laevis in King Pond control experiments at 21°C, with two different starting densities. Density = total # organisms in 300mL enclosures.

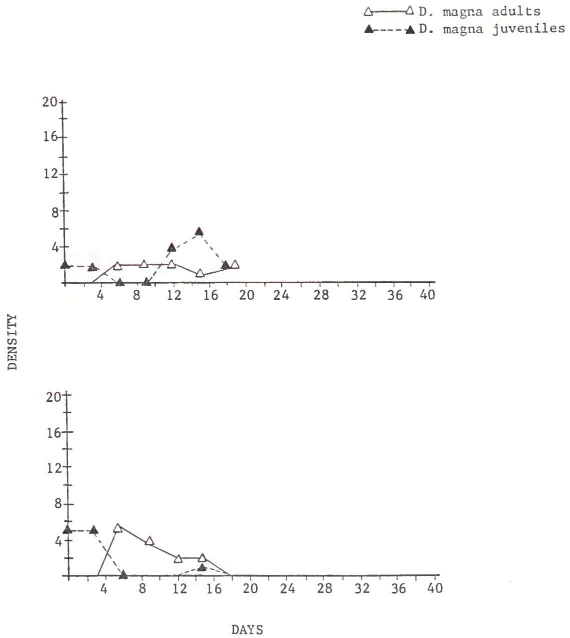


Figure 24. Population dynamics of Daphnia magna in King Pond control experiments at 21°C, with two starting densities. Density = total # organisms in 300mL enclosures.

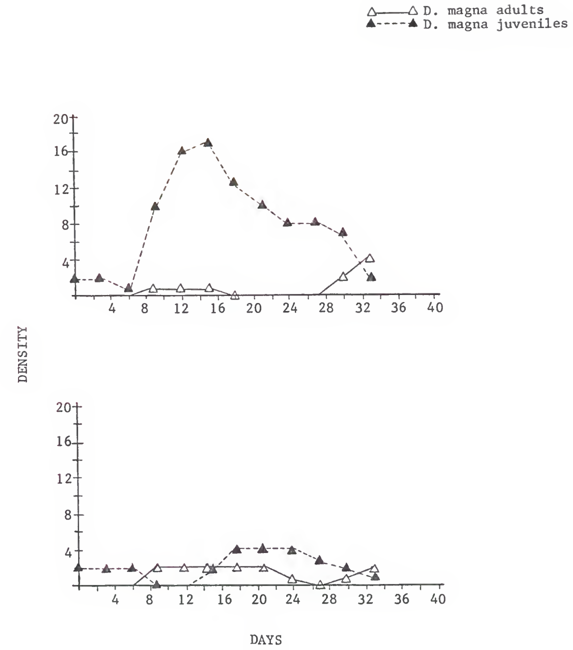


Figure 25. Population dynamics of Daphnia magna in King Pond control experiments at 27°C. Density = total # organisms in 300mL enclosures.

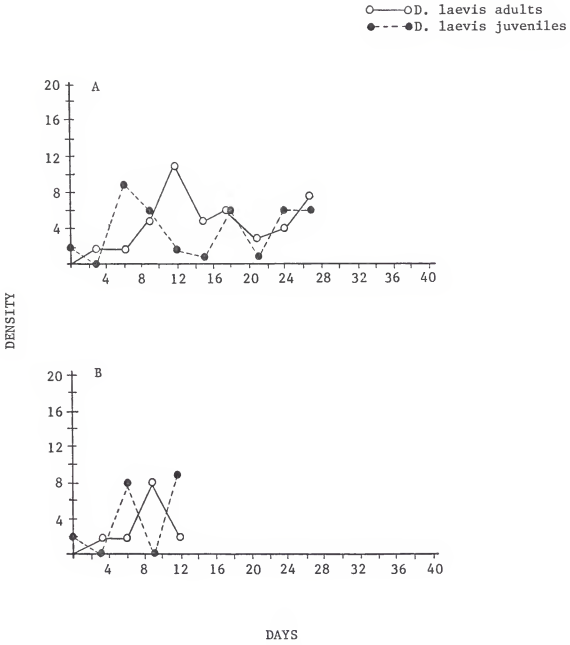


Figure 26. Population dynamics of Daphnia laevis in King Pond control experiments at 27°C. (Replicate B accidentally terminated after 12 days.) Density = total # organisms in 300 mL enclosures.

tively constant (± 2°C) throughout the experimental period. I was also able to adjust enclosure depth as surface waters warmed to keep experimental populations at or near 21°C.

Potential food (algal) concentrations in King Pond ranged from 1 x $10^1$ to 1 x $10^4$ cells/mL. All dominant algal species (those that comprised greater than 5% of the total algal population at a specific date) were small and without sheaths; therefore, it is likely that they were available as a food source for zooplankton. Gut content analysis was not performed on zooplankton since it is unlikely that these non-sheathed forms are resistant to rapid digestion. Bacterial and detrital analyses were not performed, yet it is possible that these items are also utilized as a food source by zooplankton.

Algal populations were dominated by *Chroomonas* sp. 1 and *Phaester* sp. during competition experiments at 21°C and by *Chroomonas* sp. 1, *Phaester* sp., and *Chroomonas* sp. 2 at 27°C in King Pond. All populations were always well below densities of 1 x $10^4$ cells/mL (Figures 7 and 8). Therefore, it is likely that food was limiting in the pond during competition experiments. This is supported by the fact that relative densities of zooplankton populations in competition jars in King Pond are similar to densities in laboratory competition jars (maximum relative density in King Pond jars = ca. 70 animals/L, maximum density in laboratory jars = ca. 100/L). It is also supported by density manipulations in competition jars in King Pond at 21° and 27°C. I manipulated starting densities of both species in control and experimental (competition) jars to determine if density effects had an impact on individual species. When five *D. magna* juveniles were used to initiate a control at 21°C (Figure 24), all animals had died by day 12, while all individuals reached adult size but none reproduced during this period. When two D. magna juveniles were used to initiate a control at 21°C (Figure 24), animals lived to the end of the experimental period (day 18), reached adult body sizes, and successfully reproduced. This density effect was never observed in D. laevis controls (Figures 23 and 26). When five individuals of each species were used to initiate a competition experiment, D. magna populations were excluded or nearly excluded in competition jars by day 10, while only one individual reached adult size (Figure 19). When 10 juveniles of each species were used to initiate a competition experiment, D. magna juveniles never matured and were completely excluded by day 6 (Figure 20).

When five juvenile D. magna were used to initiate controls at 27°C, all individuals had died by the first sampling period (day 3). This was also true in one competition jar; however, in its duplicate, one D. magna individual reproduced and both species coexisted until day 26, when D. magna was excluded (Figure 21). Animals lived until the end of the experiment (day 33), and they also grew and reproduced effectively when two juvenile D. magna were used to initiate controls. When two individuals of each species were used to initiate competition experiments at 27°C, D. laevis excluded D. magna by day 21, while no adult D. magna ever reproduced. Therefore, density has a less clear effect at 27°C, yet D. laevis is still a superior competitor at this temperature.

Finally, there has been much discussion of whether the impact of competition falls heaviest on adults or juveniles of a species. My data strongly suggest that this impact falls heaviest on juveniles. In almost every laboratory competition experiment, recruitment from D.

*magna* juvenile to adult body sizes is inhibited after about day 10, or after the period when juveniles used to initiate an experiment matured. That is, large numbers of *D. magna* juveniles at a sampling date are not reflected in large *D. magna* adult populations at some later date, as would be expected if all juveniles grew to adult body sizes. (Initial maturation would be expected if food levels are not critically limiting during periods of low daphnid population densities used to start an experiment as in Figure 18.) Maturation inhibition is also observed in field competition experiments, but the effect is pronounced only at 21°C. At 27°C (Figure 22), inhibition of reproduction may enhance the effect of inhibited recruitment on limiting *D. magna* populations. I did not differentiate between newly recruited adults and adults that had matured early in a laboratory experiment and had lived for long periods of time. However, in field experiments, in small jars with relatively low numbers of experimental animals, I observed that survivorship of adults was generally not inhibited, rather recruitment of adults from juvenile size classes was unlikely to occur.

In *D. magna* controls, some adult recruitment inhibition was observed, but never to a point where adults were not available for reproduction, while recruitment of *D. laevis* adults was never inhibited in either competition or control situations. Once again, these data show that, under my experimental conditions, *D. laevis* is a superior competitor when compared to *D. magna*, and it is likely that the impact of competition has its greatest influence on *Daphnia magna* juveniles.

It is noteworthy that survivorship [$\ell(x)$, the proportion of individuals surviving to age x] of individuals in life history experiments does not reflect the trends observed in competition experiments (Figures 27 and 28). In fact, at low food concentrations, survivorship curves of D. laevis generally begin to decline at a similar or earlier age than those of D. magna. There appears to be little difference between curves of the two species at high food concentrations. Two explanations seem reasonable. Food concentrations in competition experiments are significantly below 1 x $10^4$ cells/mL throughout a good portion of competition experiments, while they are kept relatively constant (near 1 x $10^4$ cells/mL) in all life history experiments. Therefore, reduced food levels may have a different impact on survivorship of the two species than that observed at 1 x $10^4$ cells/mL. Alternatively, if $\ell(x)$ curves are representative of curves at any low food concentration, then some other form of species interaction (e.g., interference competition) may influence survivorship in competition experiments. Further work needs to be conducted to solve this problem.

Figure 27. Survivorship, $\ell(x)$, curves of Daphnia magna at three temperatures (15, 21 and 27°C), and high (HF - $5 \times 10^5$ cells/mL) or low (LF - $1 \times 10^4$ cells/mL) concentrations of Chlamydomonas reinhardi. All experiments terminated after 21 days.

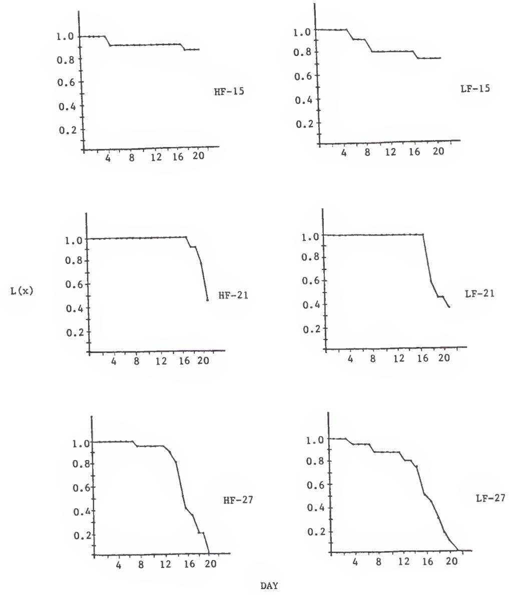
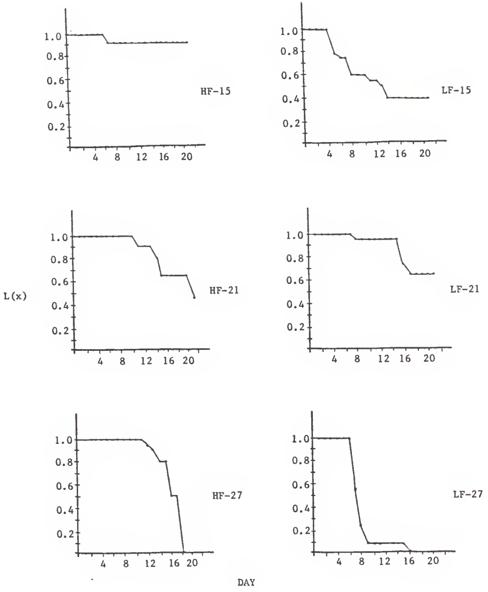

HF-15
LF-15
HF-21
LF-21
HF-27
LF-27
L(x)
1.0
0.8
0.6
0.4
0.2
4
8
12
16
20
DAY

Figure 28. Survivorship, $\ell(x)$, curves of *Daphnia laevis* at three temperatures (15, 21, and 27°C), and high (HF - 5 X $10^5$ cells/mL) or low (LF - 1 X $10^4$ cells/mL) concentrations of *Chlamydomonas reinhardi*. All experiments terminated after 21 days.



HF-15
LF-15
HF-21
LF-21
HF-27
LF-27
L(x)
1.0
0.8
0.6
0.4
0.2
4
8
12
16
20
DAY

# CHAPTER 4
# GENERAL DISCUSSION

This study shows that D. laevis outcompetes D. magna under food limited conditions at three constant temperatures and that the competitive superiority of D. laevis at 21° and 27°C is predictable from its life history characteristics at these temperatures at low food concentrations. D. laevis has a higher $r_m$ than D. magna both at high and low food concentrations at 21° and 27°C, which is a result of the ability of individuals to begin reproduction at an earlier age than D. magna individuals. At 15°C, neither animal has a fitness advantage (reproductive component) at high or low food concentrations, primarily because both species begin reproduction comparatively late in life. Yet, D. laevis is still able to outcompete D. magna at this temperature after an initial 25-day period where densities of both species are similar. Therefore, these data do not support classical r-K theory (Pianka 1978) and do not allow consistent prediction of competitive superiority, even when life history characteristics are measured at low food concentrations.

To predict the nature of zooplankton community structure from competitive interactions alone would be profoundly in error. There is abundant evidence that both vertebrate and invertebrate predation have major influences on zooplankton community structure (Brooks and Dodson 1965; Dodson et al. 1976; Hall et al. 1976; Zaret 1978) and life histories (Lynch 1980). Yet, the widespread and perhaps universal rarefaction of the genus Daphnia in subtropical and tropical aquatic habitats is interesting, particularly in light of the fact that it occurs not only in lakes that have been surveyed, but in the few ponds, including those without vertebrate predators (Mavuti and Litterick 1981 and this study) that have been surveyed. Unfortunately, the degree to which subtropical and tropical aquatic systems have been examined is not nearly commensurate with their temperate counterparts. This is an area of aquatic biology that needs greatly increased attention.

The question remains, is observed daphnid rarefaction in the subtropics and tropics a result of increased predation, temperature intolerance, substantial algal or bacterial compositional changes, competitive interactions, or some combination of these factors? Some answers to these questions follow.

It is unlikely that elevated subtropical and tropical temperatures are lethal to D. magna. In fact, the intrinsic rate of population growth of this species was highest at 27°C. Survivorship of this species was reduced at 27°C; however, a decrease in the age of first reproduction more than compensated for the effects of decreased survivorship on $r_m$. Elevated temperatures may have other, as yet undetermined, effects of large daphnid species, including D. magna. If high temperatures inhibit ephippia formation in large species, or inhibit the viability of ephippia themselves, then these species may be excluded from subtropical and tropical aquatic habitats. No work has been completed to test this phenomenon.

It is likely that temperature has a differential physiological effect within the genus Daphnia. The effects of temperature on filtering rates (McMahon and Rigler 1963; McMahon 1965; Burns 1969) and respiration rates (Richman 1958; Lynch 1977) of members of the genus Daphnia have been described. Lynch (1977) examined the influences of temperature, body size, and food size distributions on fitness of various body-sized D. pulex individuals and predicted that at 25°C (compared with 15° and 20°C), smaller bodied individuals will have a higher fitness associated with feeding efficiency (= food intake/metabolic demands), regardless of food size distributions, than larger bodied individuals (that is, optimal foraging size is always smallest at 25°C). These data were calculated for different body sizes of only one species. However, if they are applicable to different species within the genus, they suggest that smaller bodied species may be more efficient at obtaining food from an environment at elevated temperatures, and utilizing this food for metabolic and reproductive requirements.

My data support the contention that there may be interspecific body-size fitness changes with temperature. A decrease in the body size at maturity is a characteristic of most populations of food limited cladocera (Lynch 1979). At 15° and 21°C in this study (Figure 29), decreases in body size at maturity of both species with limited food resources are similar (ca. 15%, $p<0.25$ for D. magna and $p<0.35$ for D. laevis). However, there is a 17% decrease in D. magna body size at maturity with limited food resources at 27°C ($p<0.20$) and only a 7% decrease in D. laevis body size ($p<0.40$). Changes of course are not significantly different ($p>0.05$), but their consistency does indicate that food limitation does have an influence on body size at maturity and that this influence has a greater impact on larger animals at higher temperatures.

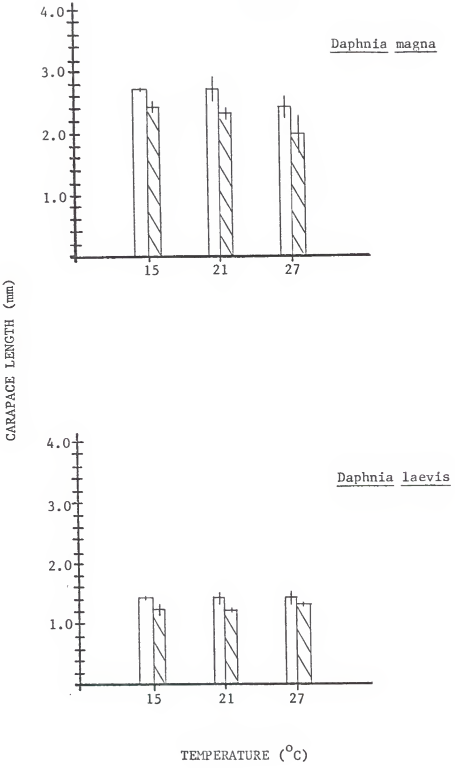


Figure 29. Body-size (carapace length) at first reproduction of *Daphnia laevis* and *D. magna* at high (open bars) and low (hatched bars) food concentrations and at three temperatures.

Relatively few algal compositional analyses of subtropical and tropical ponds and lakes have been completed. The few data that do exist suggest that, regardless of trophic state, phytoplankton populations are generally more stable in subtropical and tropical systems than in temperate lakes. In fact, the typical spring bloom of algae that occurs in most temperate lakes and coincides with high "edible" algal diversity (nonsheathed Chlorophyta and Bacillariophyta) (Wetzel 1975) as well as high zooplankton abundance and diversity does not occur in tropical lakes that have been studied.

In Lake Kinneret, Israel, a relatively deep (maximum depth, 42 m), mesotrophic lake where temperatures range from 15° to 30°C yearly, the winter algae are dominated by few species of *Peridinium*, *Microcystis*, and *Melosira*, while the summer algae are dominated by *Elakatothrix*, *Cosmarium*, *Tetraedron*, and *Chroococcus* (Berman et al. 1971). This lake has no *Daphnia* species, while the zooplankton throughout the year are dominated by several rotifers, *Mesocyclops*, *Thermocyclops*, and small populations of *Diaphanosoma*, *Bosmina*, and *Ceriodaphnia*.

The well-studied Lake George, Uganda (Burgis and Walker 1972; Burgis 1969; Burgis et al. 1973), is dominated throughout the year by the blue-green algae *Microcystis*, *Aphanocapsa*, *Anabaenopsis*, and *Lyngbya*. This lake is hypereutrophic, shallow, and exhibits a yearly range of temperatures of 25°–30°C. The thermal regime of the lake is compressed into 24-h periods, and the relative climatic stability, as well as the stability of nutrient kinetics of the lake, inhibit any successional algal changes, and enhance the dominance of the algal community by a few Cyanophyta (Ganf and Viner 1973; Burgis 1977). Lake

George is dominated by the copepods Thermocyclops and Mesocyclops, while small populations of Daphnia barbata occur periodically.

The algae of Lake Chilwa, Malawi, are dominated throughout the year by Oscillatoria, Anabaena, Arthrospira, and Spirulina. This shallow, turbid lake has a temperature range of 15°–30°C and is considered hypereutrophic (Kalk et al. 1979). A lake with similar temperatures (17°–29°C) is Lake Sibaya, South Africa, a deep (40 m), oligo-mesotrophic lake whose net phytoplankton are dominated by Closterium, Synedra, Anabaenopsis, Melosira, and Anabaena. Nannoplankton concentrations in Lake Sibaya range from $1 \times 10^3$ to $5 \times 10^3$ cells/mL throughout the year (Hart and Hart 1977; Allanson 1979). Unfortunately, nannoplankton have only been enumerated and not specifically identified in Lake Sibaya. The zooplankton of both of these lakes are dominated by calanoid and cyclopoid copepods, small populations of the cladocerans Moina, Bosmina, and Ceriodaphnia, and several rotifer species.

Perhaps the most complete phycological analysis of a tropical lake has been conducted by Lewis (1978a) on Lake Lanao, Philippines. The study concentrated on the number of species, dominance and relative abundance, compositional overlap between environments, and the distribution of tropical phytoplankton communities. These data are the most useful for determinations of algal community structure and the impacts that this structure may have on zooplankton species diversity.

Lake Lanao is a clear (1% light compensation point = 12 m), deep (112 m) lake with yearly temperatures ranging from 21° to 24°C. The lake is relatively productive but maintains its high transparency due to low amounts of nonliving suspended matter and great amounts of mixing (Lewis 1978a). The common algal species of this lake occur throughout the year, and half of these species belong to the Chlorophyta. The Cyanophyta compose most of the remainder of dominant algae, and make up greater than 90% of the algal standing stock in Lake Lanao.

I used Lewis' (1978a) data to determine the concentration of algal cells available as a food source to cladoceran zooplankton in Lake Lanao. Criteria for selection included cells that would be considered nonresistant to digestion (nonsheathed), had a volume of less than 1000 $m^3$, and did not belong to the Cyanophyta. Of the 20 most abundant algal taxa in Lake Lanao, ten, including three of the most abundant algal taxa in the lake, fit all criteria. The average, "edible," algal abundance in Lake Lanao from July 1970 to October 1971 was $9.3 \times 10^3$ cells/mL. This number may be low if some blue-greens are available as food sources, but is certainly near or below levels that may be considered limiting to the large, temperate *D. magna*.

Lewis (1978a,b) suggests that all of the features of Lake Lanao's phytoplankton are pantropical, but that there are major differences between tropical lakes and comparable temperate lakes. In lake Lanao, the biomass of all autotrophs, as well as major individual phytoplankton taxa, vary less over a year than autotroph biomass in temperate lakes, primarily due to winter biomass losses in temperate systems. Also, in temperate lakes, the number of algal genera is significantly higher than in the tropical lakes that Lewis studied, and this is primarily due to the importance of the Chrysophyceae in temperate lakes and their absence in most tropical lakes.

All of these studies suggest that tropical, and to some extent subtropical, lakes share several characteristics. Regardless of trophic state, they have a narrow range of temperatures, abundant representation of the Cyanophyta, and generally more stable algal species composition than temperate systems. Unfortunately, most works do not address relative abundances of phytoplankton, either in individual or biomass units, and little mention is made of algal edibility, although it may be assumed that edibility is low when the Cyanophyta dominate lake phytoplankton (Arnold 1971; and a review in Porter and Orcutt 1980). If, in fact, edible algal abundance or biomass is in some equilibrium with indigenous herbivore populations (zooplankton or fish), and this equilibrium is maintained throughout the year as evidenced by stable yearly species composition in tropical lakes, then it may be assumed that these environments, or their algal populations at least, are at or near carrying capacity for the organisms found in them and that this carrying capacity is below that necessary for organisms that do not occur there, particularly large species of Daphnia. This is certainly a tautological argument; yet evidence from my work shows that this is the case in King Pond. Algal populations are at a level where a large temperate cladoceran, D. magna, has a significantly reduced reproductive fitness compared to its smaller subtropical relative, D. laevis; and, of course, D. laevis outcompetes D. magna when the two species share limited resources. It is also evidenced by the fact that D. magna laboratory control densities are always lower than D. laevis control densities (Figures 14, 15, 17), when both species have reached some apparent equilibrium (with the exception of D. laevis at 15°C, Figure 17).

The outcome of competition within the cladocera has received much attention. Generally, smaller species tend to be better competitors than larger species (Dodson 1974; Neill 1975; Lynch 1978, 1979; Goulden et al. 1982b; Smith and Cooper 1982) although there are exceptions (Sprules 1972; Allan 1977). More importantly, the effects that competition has on zooplankton community structure are frequently influenced or mediated by predation (Sprules 1972; Dodson 1974; Kerfoot 1977, 1978; Jacobs 1978; Lynch 1979; Threlkeld 1979; DeBernardi and Manca 1981), abiotic, or other biotic factors (Allan 1977; Lynch 1978, 1979; Seitz 1980; Hanski and Ranta 1983). Unfortunately, most analyses of competitive interactions within the cladocera, and particulary between species of Daphnia, are plagued by poor design or incomplete analysis. Outstanding among these are studies that draw conclusions about the results of competitive interactions from very short-term manipulative studies (Sprules 1972; Smith and Cooper 1982; Cooper and Smith 1982; Goulden et al. 1982b). All of these suggest that a species is superior if it depresses a competitor without actually causing exclusion. A good example of this problem is found in Goulden et al. (1982b), where it is proposed that D. galeata has a greater effect on Bosmina than the opposite, based on populations sizes of the two species in competition experiments after 30 days. Yet, Bosmina eventually suppresses D. galeata populations, often nearly to extinction, in these same experiments after 65 days. Goulden et al. conclude by stating: "Over exploitation of food resources by a competitive dominant population can provide an opportunity for a less successful competitor to coexist and even become the numerical dominant" (1982b:1788). I suggest that when a species sharing a limited resource is completely dominated (excluded) after a period of time by another species also sharing that resource, the excluded species should be considered competitively inferior regardless of the nature of the population dynamics of the two species prior to exclusion.

There are other problems with Goulden's study as well. Unequal feeding regimes within and between species are used in life history experiments, and for no apparent reason, only the outcome of competition between *D. magna* and *D. galeata* at high food levels is reported. The results of competition between the two species at limited food levels would have been far more interesting and useful for comparative purposes.

My work shows that, for *D. laevis* and *D. magna*, short-term competition experiments shed little light on the final outcome of interactions between these two species. In fact, erroneous conclusions could easily be drawn using results of 10 to 30-day experiments in this study. Fortunately, research exists where long-term analysis (to exclusion) of competititve interactions has been completed. These studies show how interactions may influence zooplankton community structure and may be used to support evidence that implicates competition as a major structuring force in tropical zooplankton communities.

DeMott (1983) examined the seasonal succession of two *Daphnia* species, *D. rosea* and *D. pulicaria*, in field enclosure studies in Lake Mitchell, Vermont. He suggested that succession was the result of competitive interactions. Dominance of the zooplankton community by *D. pulicaria* in summer and fall was due to its ability to utilize "resistent" algae (gelatinous greens) as a food source more efficiently than

*D. rosea*. *Daphnia rosea* dominated the plankton in spring and early summer, when the algae were composed of edible flagellates, but no reason was found for *D. rosea*'s competitive success during this period when food (edible flagellate) concentrations were, according to DeMott, abundant. Correlation analysis showed no relationship between competitive success and water temperature. However, examination of their data shows that *D. pulicaria* is only inhibited in spring and early summer, when water temperatures are below 20°C and food levels are in fact, relatively low (1 x $10^3$ to 1 x $10^4$ cells/mL). During the summer and fall, when water temperatures range from 21° to 25°C, *D. pulicaria* is the dominant daphnid. Enrichment experiments show that *D. rosea* is food limited during this period, when the algae are dominated by resistant forms. I propose the following scenario then as an alternative explanation for the daphnid succession in Lake Mitchell. In spring, at low water temperatures and food concentrations lower than 1 x $10^4$ cells/mL, *D. rosea* is able to reproduce more rapidly than *D. pulicaria* and becomes the dominant daphnid in the pond; that is, *D. rosea* is competitively superior at low food concentrations and low temperatures. As temperatures rise, the reproductive advantage shifts, either to *D. pulicaria* or to neither species, but *D. pulicaria* dominates the plankton due to its ability to utilize resistant algal species as a food source. To confirm this scenario, simple life history analyses, such as I have performed for *D. laevis* and *D. magna*, could be utilized to test genotypic (or phenotypic) differences in growth and reproductive rates as a function of temperature. These data do not exist, but there is evidence that *D. rosea* is favored at lower temperatures. *Daphnia rosea* filtering rates are highest near 14°C (Kibby 1971), while the highest egg production rates and instantaneous rates of population increase for this species occur between 15° and 18°C (Dodson 1972). Daphnia pulicaria populations, however, increase more rapidly at 19°C than at 15°C (Slobodkin and Richman 1956), and this species had its highest $r_m$ at temperatures above 22°C in Wintergreen Lake, Michigan (Threlkeld 1979).

In an elaborate and elegant set of experiments, Neill (1975) examined the interactions between zooplankton, their predators, their food resources, and the community structure that results from these interactions. Using microcosms to analyze the interactions, he found that stable communities of zooplankton and algae (food) developed after 7 months of continuous species introductions and that these communities consisted of three cladocerans, an amphipod, and five species of algae. These communities persisted in stable environmental (laboratory) conditions regardless of the nature of further introductions. The dominant zooplankton species in these communities was Ceriodaphnia, and this organism was the major microcosm organizer and competitor. In fact, it was competitively superior when compared to two large daphnid species, as well as several other cladocerans. The only time that microcosms were amenable to invasion was when Ceriodaphnia populations were reduced by predation. When the influence of predation was removed, Ceriodaphnia returned as the community organizer. The competitive superiority of Ceriodaphnia over other, larger daphnids was apparently due to the influence that the organism had on juveniles of other species with whom it shared similarly-sized food resources. This phenomenon was confirmed in life history survivorship studies.

Neill suggested that his stable laboratory conditions were probably not representative of natural ecosystems but shed light on competitive interactions in a very narrow setting. I suggest that, from tropical temperature and a few algal data mentioned earlier, Neill's microcosms, at least in part, closely resemble tropical lakes. These lakes are characterized by few zooplankton species and few edible algal species. As mentioned earlier, these zooplankton species may, as Neill stated, be the species that outcompete others for limited resources, as they maintain positive growth rates at sufficiently low resource concentrations at which their competitors can no longer be sustained. In a temperate system where environmental conditions are not nearly as stable, such as Lake Mitchell (DeMott 1983), there is good evidence that increased species diversity and species succession that occurs seasonally, and that this seasonal species succession is intimately associated with temperature and food resource fluctuations. That these fluctuations have a major influence on zooplankton life history and competitive abilities has been evidenced in the experimental work completed for this study.

Two mechanisms then may be proposed for maintaining daphnid species diversity in temperate aquatic habitats and rarefying it in the subtropics and tropics. Large and frequent temperature fluctuations are a common characteristic in temperate lakes and generally rare in tropical lakes. The fluctuations may shift competitive superiority from one species to another. There are undoubtedly temperature dependent species-specific peaks in filtering rates in Daphnia (Burns 1969; Kibby 1971), and this study has shown differential species responses of $r_m$ to temperature. There is also evidence that respiration or metabolic rates are a function of species body size and temperature (Lynch 1977). That filtering rates, $r_m$, and respiration or metabolic rates are intimately associated with each other is highly likely, and therefore the combination of these factors (fitness) is greatly influenced by temperature. In fact, the effect of temperature on the fitness of two zooplankton coexploiters (Ceriodaphnia and Daphnia) has received further support by Lynch (1978), who showed that the outcome of competition between the two species is primarily a function of temperature. Yet, in this study, D. laevis always outcompetes D. magna under stable, limited food regimes, regardless of temperature. It is noteworthy that competitive exclusion generally takes longer at the two extreme temperatures used here than at 21°C. This may simply be due to long-term acclimation of laboratory animals to 21°C or due to increased stress imposed by extreme temperatures on juveniles of either species, but differentially on D. laevis (Figures 27 and 28). In King Pond at 27°C, it may also be due to the addition of one algal species or to changes in the rates of diffuse competition. A potential competitor, Diaptomus floridanus, has peak populations during July and August, at elevated temperatures, and it is possible that this increase in copepod density has a negative impact on D. laevis, with whom it may compete directly for resources in King Pond over long periods of time. Regardless, the evidence here does not implicate temperature alone as the sole determinant of fluctuating competitive abilities and species diversity in natural environments.

That temperature has a major influence, however, is likely. I suggest that temperature greatly influences the dynamics and structure of the algal community. I have already noted the relative stability of algal populations in tropical habitats. Granted, other factors play a role in this stability (nutrient dynamics, light intensity, photoperiod, grazing rates); yet stable tropical temperatures may be a critical factor. Tilman et al. (1981), have recently shown that differential nutrient uptake abilities exist between phytoplankton species and that these species-specific abilities are easily shifted or changed with temperature changes. This phenomenon was then extended to the community level, where variations in temperature can allow long-term persistence of many algal species, and where this phenomenon actually supplied an answer to Hutchinson's paradox. One may posit then, that in a system that lacks significant temperature variation, algal diversity may be drastically decreased due to enhanced competitive interactions between species that are constantly at or near environmental carrying capacity. These characteristics, of course, are common to tropical aquatic habitats.

The implications of this stability and resultant decreased diversity at the primary producer level should then have ramifications throughout the food chain. I suggest that one of these ramifications is decreased zooplankton species diversity. This decrease may be particularly manifested in the genus *Daphnia*, the members of which may be well adapted to environments where a high quality, abundant, but short-lived food source is available (Porter et al. 1983; Richman and Dodson 1983). Tropical aquatic habitats, frequently dominated by blue-green algae and with relatively low densities of edible algae may be more suitable to zooplankton that do not share *Daphnia*'s design constraints, such as metabolically costly rejection behavior or lack of ability to selectively filter various particle sizes (Porter et al.

1982, 1983; Richman and Dodson 1983). These abilities, or lack of them in the case of rejection behavior, belong to zooplankton including Bosmina (DeMott and Kerfoot 1982), Ceriodaphnia (Webster and Peters 1978; Pace et al. 1983), and many copepods (Porter et al. 1982; Richman and Dodson 1983), all common elements of tropical zooplankton communities.

The characteristics of tropical zooplankton communities are likely, at least in part, a function of the selective pressures imposed by stable temperature and resource regimes. However, small body size has also been shown to be an excellent device for avoiding vertebrate predators (Hall et al. 1976; Lynch 1977, 1980). The fitness of organisms that reach maturity early in life and at small body sizes is maximized when predation by vertebrates is intense, while organisms that mature relatively late in life and at large body sizes are more fit when invertebrate predation is intense (Lynch 1977). The nature of predatory pressures in subtropical and tropical lakes compared to temperate lakes is not well resolved. Of interest, however, are the body sizes of zooplankton in subtropical and tropical aquatic habitats where vertebrate predators are absent and where predation pressure, if it exists, should select for organisms that mature late and at large body sizes. Only two examples are available, this study and data from Mavuti and Litterick (1981). Both studies cite ponds free of vertebrate predators, where a moderate sized daphnid, D. laevis, is abundant. Obviously, much more detailed analysis of tropical, vertebrate predator free aquatic habitats should be completed to shed greater light on the relationship between selective pressures in these systems, and the structure of their zooplankton communities.

This work shows that, in the absence of predation pressure, maximal reproductive and competitive fitness are not accrued by the largest body-sized cladoceran individuals and allows for predictions to be made about the body-sizes of cladoceran zooplankton in, and community structure of, subtropical and tropical vertebrate-free aquatic systems. I suggest that the pelagic of tropical aquatic habitats are comparatively simple, stable environments where zooplankton exist near carrying capacity for long periods of time, and where few opportunities for niche partitioning exist. The result is a rarefied community of organisms that are K-selected, but where this K-selection does not involve the usual reproductive and growth trade-offs. Rather these organisms possess mechanisms for dealing with the usual selective pressures found in an aquatic environment (e.g., predation), as well as selective pressures imposed by low but constant and predictable food supplies and constant, elevated temperatures.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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